EXPERIMENTS ON SEED DISPERSAL AND DEPOSITION PATTERNS OF EPIPHYTES.- THE CASE OF *TILLANDSIA DEPPEANA* STEUDEL (BROMELIACEAE)

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Seed dispersal is one of the most important aspects in the life cycle of flowering plants. This process can help to maintain or increase their numbers, colonize new sites within or outside their communities (Harper, 1977; Pijl, 1982), and increase gene flow (Beattie, 1978). Nevertheless, the presence or absence, and the density of a population, depends not only on the availability of seeds, but on a series of deterministic events within an environment. One of these is the frequency of safe sites, which are microsites that provide the precise conditions requered by a particular seed (Harper, 1977).

The density of seedlings will most often be determined by the number of microsites available; in most parts of a plant's range, seed will outnumber microsites. The availability of microsites places a ceiling on the population density of seedlings (Crawley, 1983). The precise properties of germination microsites or safe site differ from species to species, but it must provide all the requisites of germination, root penetration and leaf expansion. Since the number of microsites can only be defined in relation to the requirements of a particular species, there can be no single parameter such as "microsite density" (Crawley, 1983). The maximum number of seeds germinating on a given area will be determined by the size and shape of the seeds relative to the surface roughness, and by many other factors (Harper et al., 1970; Harper, 1977; Crawley, 1983). Thus, while the number of microsites may well limit the rate of seedling recruitment, the number is probably impossible to estimate.

The knowledge of seed deposition patterns and safe site availability are important to the increasing number of studies on plant population dynamics, but technical difficulties have hindered collection of such information (see Werner, 1975, for review). Information concerning seed deposition patterns and inferences on the number of available safe sites could result from experimental approaches (Werner, 1975), or from studies on the spatial distribution of individuals within a population, assuming that greatest abundance reflects optimal sites for seed deposition, germination, and seedling development (García-Franco & Peters, 1988).

Seed dispersal studies have been carried out mainly for terrestrial plants (i.e., Werner, 1975; Conant, 1978; Watkinson, 1978; Magraw & Musselman, 1979). These authors have defined and described the appropiate techniques to mark and recapture seeds, but have not considered the problem for epiphytes. Eighty four percent of epiphytic plants are anemochorous. Most epiphytes produce high seed numbers that result in dense seed rains, increasing the probability of reaching an optimal microsite (Madison, 1977). For example, an orchid capsule may contain as much as 5 millon seeds (Dressler, 1981), a capsule of Cycnoches chlorochilon (Orchidaceae) contained 3,770,000 seeds (Dunsterville, 1962), and the infrutescences of Tillandsia deppeana (Bromeliaceae) contain a mean of 3,834 seeds per plant (unpublished data). Which is the fate of all those seeds? Some authors consider that epiphytic plants require specific host trees for their development and that they are more abundant on particular parts of the host's crown (Valdivia, 1977; García-Franco & Peters, 1988); nevertheless, nothing is known about their seed deposition pattern or about the probability of a seed in reaching an optimal microsite.

This paper describes an experiment to determine the seed deposition pattern of Tillandsia deppeana Steudel (Bromeliaceae) on its prefered host tree, Liquidambar styraciflua L., as well as the probability of T. deppeana seeds in reaching an optimal microsite on another specific host tree.

DESCRIPTION OF THE STUDY SITE

The site.- Field work was done in Parque Ecologico F. X. Clavijero, 2 km SE of Xalapa, Veracruz, Mexico; at 1,280 m above sea level. The park has a small area of cloud forest, including Tillandsia deppeana as a common epiphyte, and an old orchard (Ortega, 1981). Park topography is very irregular, with a deep layer of clay-sandy soil. Climate in the area is humid-temperate, with rain fall distributed throughout the year. Mean annual temperature is 17.9°C and total annual precipitation is 1,515 mm (García, 1973; Soto, 1986).

The plant.- Tillandsia deppeana is an epiphyte that reaches 80 cm in height (including inflorescence spike). It has a funnelform rosette shape, green leaves, erect scape, short-pinnate inflorescences with pink to red spikes, blue-violet flowers, and capsular fruits. This species is endemic of Mexico, distributed in cloud and pine forests, between 1,080 and 1,800 above sea level, in the states of Tamaulipas, Hidalgo, Puebla, Veracruz and Oaxaca (Smith & Downs, 1977; García-Franco, 1987). As in most bromeliads, sexual and asexual (offshoots) reproduction are present in T. deppeana, but because it only produces one offshoot, the later is not considered as important as in other species of the group. Fifty three percent (53.57%) of the T. deppeana individuals in the study area have L. styraciflua as host tree, the rest of the individuals are scattered on species of *Quercus* and other species; 30.61 % of the *T. deppeana* individuals on *L. styraciflua* are localized in the 3-11 m height range; mean distance between *L. styraciflua* individuals is 14.24 $\pm$ 7.5 m (n = 20); mean distance between all host tree species of *T. deppeana* in the area is 11.78 $\pm$ 6.10 m (n = 55) (unpublished data).

METHODS

The experiment was accomplished during the first two weeks of March, 1988, corresponding with the seed dispersal period of *T. deppeana*. Field work days were characterized by strong winds, originated by the north-south displacement of the cold fronts. The combination of the cold air coming from the north of the continent and the warm air of the Gulf of Mexico, causes great environmental humidity and many days with mist and fine rain. These are the prevailing winter conditions for this region.

The firts part of the experimental design consisted on the collection of 8,500 seeds of *T. deppeana* (a mean of 3,839 seeds per plant). These seeds were marked with a fine fluorescent powder (USR Optonix, Inc.) and placed on a tray suspended at 6.90 m above ground on a branch of the *L. styraciflua* tree used as "origin". The tray was left in that position for five days. The second part of the experimental design was done simultaneously, and consisted on placing six chains of seed traps, each chain was made of four or five rectangular pieces of cardboard (42 cm x 30 cm) covered with a sticky surface (stripes of maskin tape), representing a capture surface of 3.40 m2. The traps were placed at different heights (between 6.90 m and 11.0 m) and distances (between 8.80 m and 28.0 m) from the "origin tree", suspended with lenghts of fishing line (Figure 1). All traps were close to *L. styraciflua* individuals, which are the most common host tree for *T. deppeana* in the area (Figure 1). At the end of the five days, the tray was recovered and the remaining seeds were counted. The seed traps were removed from their positions and the number of fluorescent marks on the sticky surface were recorded with the aid of a U.V. lamp (UVP, Inc., model UVL-21).

RESULTS AND DISCUSSION

At the end of the five day period, 3,849 seeds remained in the tray and 4,651 were dispersed. Of the later seeds, 171 were captured on the 3.40 m2 trap surface. The probability of a seed from the tray in reaching a trap was 0.037. If we consider that the crown surface area of a *L. styraciflua* tree is roughly 87.78 m2 and that our sample area was 3.40 m2, then we should expect that 4,414.8 seeds could be deposited per tree; this is equivalent to the number of seeds produced by one and a half *T. deppeana* individuals. Despite the high number of seeds that could theoretically reach a given tree, we only found a mean of 4.2 $\pm$ 3.6 *T.*

deppeana plants per host tree, which should produce annually, ca. 15,336 seeds.

All captured seeds were registered between 3.30 m and 10.64 m above ground; the highest percentages were between 3.55 m and 6.50 m (49.7%), and between 7.55 m and 10.50 m (44.44%). These data reinforce our observation that the highest number of T. deppeana individuals fall between the 9.0-11.0 m height range.

Concerning seed dispersal distance, we captured 62 % of the marked seeds between 8.80 m and 15.0 m away from the "origin tree", and 38 % between 24.5 m and 28.0 m. McWilliams (1974) mentiones that a Tillandsia fasciculata seed remained airborne for 12 sec; the greatest flight distance we were able to measure for a marked T. deppeana seed was 35.0 m, airborne time should exceed the above report. The distance where the highest number of seeds were captured (8.80-15.0 m) closely resembles that of the mean distance between L. styraciflua host trees (14.23 m), or the distance between all host trees species of T. deppeana in the area (11.78 m); thus, there should be no difficulty for seeds to reach a host individual. It has been noted by several authors (see McWilliams, 1974) that the Tillandsioideae have the greatest geographical range of the three bromeliad subfamilies, and that airborne time is highly correlated with potential dispersal distance. It seems to us that, eventhough the Tillandsioideae have a wide range, individual species have relatively restricted geographical ranges (with the exception of Tillandsia usneoides L. and its forms and varieties). Under normal atmospheric conditions, the distance covered by seeds dispersed by wind will fall within the range of the population. Long-distance dispersal events should result from extreme atmospheric conditions, i.e. hurricans, and the low probability that a seed will be deposited on a safe microsite.

CONCLUSION

The method utilized, both cheap and easy to use, allowed us to infer T. deppeana's seed dispersal and deposition patterns. T. deppeana individuals allocate high amounts of energy to the production of propagules, which eventually will have a low probability of success. Low success, whether due to the lack of safe microsite, or to the failure of seeds in reaching a suitable host tree, makes us wonder that, if it wasn't for vegetative reproduction, the density of T. deppeana should certainly be lower than observed.

After analyzing our results, it is tempting to conclude that, a) available safe microsites for T. deppeana are scarce, only 4,2 plants per host tree, when theoretically 4,414.8 seeds could be captured by the 87.78 m2 surface of the host tree, b) these sites are localized between 4.0 m and 11.0 m above the ground, and c) there should be no difficulty for seeds to reach a host tree, most seeds were captured between 8.80 m and 15.0 m away from the seed source, and mean distance between host trees is 14.23 m.

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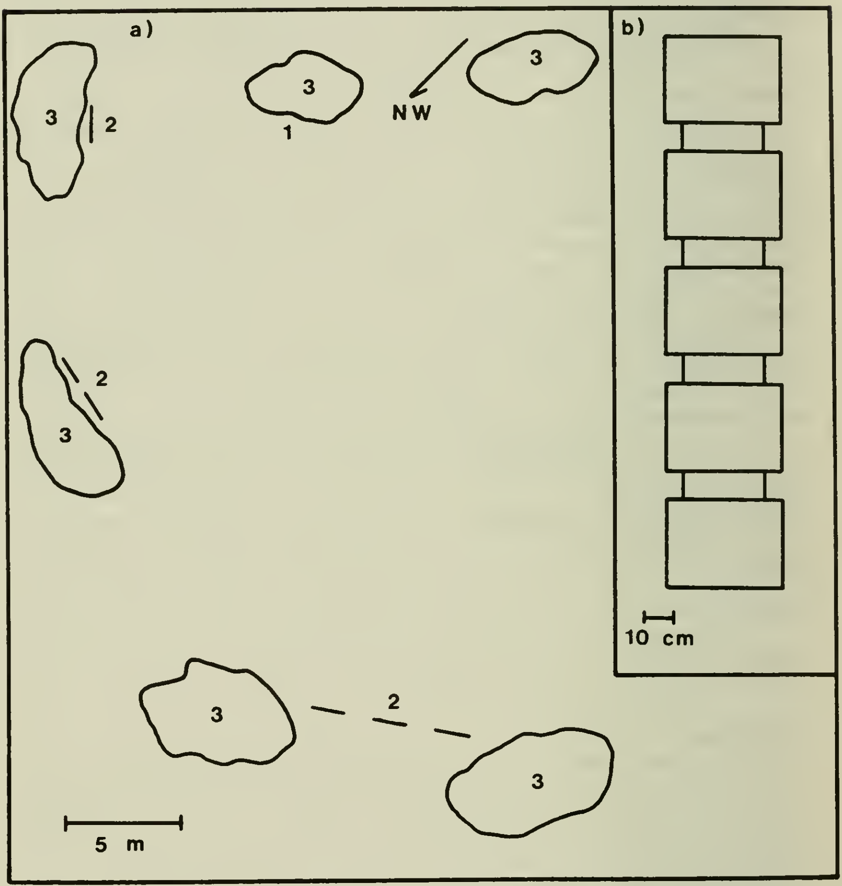

Figure 1. a) "Origin tree" (1), seed traps (2), *Liquidambar styraciflua* individuals (3). Arrow shows wind direction. b) Example of a seed trap.